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Physiological, temporal, and environmental determinants of forage fish caloric content in the Gulf of Mexico

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by

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Abstract

Within the Gulf of Mexico, forage fish species serve as an important link between lower trophic levels and higher trophic levels, supporting economically valuable predator fish, birds, and mammals. Despite the key ecological role of forage fish, fisheries management efforts are often directed elsewhere; as a result, input data for fisheries models is unavailable for many forage fish species. To fill this knowledge gap, we sought to produce species-specific caloric content values for four forage fish species in the Gulf of Mexico: Atlantic croaker (*Micropogonias undulatus)*, white trout *(Cynoscion arenarius),* bay anchovy (*Anchoa mitchilli*), and gulf menhaden (*Breevortia patronus*). We additionally investigated the impacts of body length, month of collection, as well as Mississippi River discharge to determine the response of caloric content to physiological, temporal, and environmental variation. Using bomb calorimetry, we were able to determine the dry energy density of the four forage fish species. Additionally, the dry varied by month, with dry energy densities dropping during and after migration. Furthermore, the dry energy densities of gulf menhaden and Atlantic croaker were positively correlated with fork length. There was also a limited positive relationship between river discharge and dry energy density. Ultimately, our species-specific caloric content values for forage fish in the Gulf of Mexico add much needed specificity to current fisheries models, especially since our caloric content values are available for a variety of temporal, environmental, and physiological conditions.

Introduction

The Gulf of Mexico (GOM) is home to some of the most productive fisheries in the United States, both in terms of biomass and economic value. In aquatic ecosystems, forge fish provide an important link between lower trophic levels, such as plankton, and higher trophic levels, such as predator fish, bird, and mammal species (Geers et al., 2016; Lamb et al., 2020; Oshima & Leaf, 2018; Sagarese et al., 2016). In the GOM, these vital forage fish species include Atlantic croaker (*Micropogonias undulatus)*, white trout *(Cynoscion arenarius*), bay anchovy (*Anchoa mitchilli*), and gulf menhaden (*Breevortia patronus*). Larval and juvenile stages of these species are found within the coastal and estuarine areas of the GOM (Nye et al., 2011; Shaw et al., 1988; Sheridan, 1978). In these life stages, individuals mainly feed on zooplankton; however, consumption of fish and larger invertebrates increases as individuals reach adulthood (Akin & Winemiller, 2013; Byers, 1981; Chittenden & McEachran, 1976; Robinson et al., 2015; Sheridan, 1978). Furthermore, each of these species participates in seasonal migrations between coastal and offshore habitats (Akin & Winemiller, 2013; Byers, 1981; Chittenden & McEachran, 1976; Griffith & Bechler, 1995). As a result, forage fish are not only primary conduits of energy transfer from primary and secondary production to higher trophic levels, but also have the potential to act as a direct link between estuarine and oceanic ecosystems, moving biomass, nutrients, and energy during their annual migrations.

Despite the valuable ecological role forge fish play within the GOM, most fisheries management efforts are focused on economically valuable game fish and fish harvested for consumption. However, ecosystem modelling is a fisheries management tool increasing in prevalence to better understand the suite of factors impacting game and commercial fisheries. Models such as

Ecopath with Ecosism enable resource managers to understand trophic interactions that impact these fisheries of interest. Beyond trophic interactions, models enable managers to evaluate the impacts of potential policy and make informed decisions about future management practices (De Mutsert et al., 2017). However, these models are only as reliable as the data that informs them and providing detailed input data about other components of the ecosystems is vital for model accuracy.

Currently, biomass of each trophic level is the primary variable used in fisheries ecosystem models, as it has the greatest effect on abundance and catch limits (the most common output values in Ecosim) compared to other input variables (Susini & Todd, 2021). However, the use of biomass in ecosystem modeling overlooks the intricacies of prey quality. Bioenergetics models often assume energetic equivalence between biomass units of different species and have the potential to misrepresent predator biomass if prey quality differs between species or time of year, even when prey biomass remains steady (Johnson et al., 2017; Spitz et al., 2010; von Biela et al., 2019). Furthermore, sensitivity analyses have found that final predator body weight was most sensitive to caloric content of prey; a +-10% change in caloric density resulted in +24.3% -22.1% change in final body weight for fisheries of interest (Aydin et al., 2005). Ultimately, the inclusion of prey quality through data such as calorie content can refine model outputs and increase accuracy over using biomass data alone.

The objective of this study was to use bomb calorimetry to measure the dry energy density (calories/g) for gulf menhaden, Atlantic croaker, bay anchovy, and white trout. Additionally, we evaluated if the dry energy densities (calories/g) of gulf menhaden and Atlantic croaker are related to variation in fish length, age class, month, or magnitude of Mississippi River discharge. These data contribute to a greater understanding of fluctuations in prey quality in the GOM, which can be used to improve existing ecosystem models of fisheries biomass in the GOM.

Methods

Obtaining fish samples

Gulf menhaden (n = 118) were sampled from Texas, Louisiana, and Alabama from March to November 2017 from fishery-independent gillnet sampling efforts conducted by the fisheries management agencies for each state. Each agency employs gillnets for sampling using the same series of panels with identical mesh sizes: two to four inches in 0.5” increments. Further independent sampling for gulf menhaden (n = 72), Atlantic croaker (n = 129), white trout (n = 30), and bay anchovy (n = 74) was done from October 2016 to August 2022 in Mississippi waters, using a seine net.

Sample Preparation and Processing

Fish were weighed (W, g) and fork length, mouth to tail fork (FL, mm), or total length, mouth to tail tip (TL, mm) was recorded. It was not possible to determine sex of the collected specimens because fish were frozen within hours of collection. In the laboratory, the fish samples were completely homogenized in a commercial blender and then placed in a deep freezer (-20°C) for 30 minutes and freeze dried for at least 48 hours. We ground each freeze-dried sample into a powder, formed the sample into a pellet, and combusted each pellet in a calibrated Parr 6100 Bomb Calorimeter to determine dry energy density (calories/g) of each sample. Calibration with a benzoic acid tablet was done for every 10 samples run. Bomb-calorimetry measures the amount of heat released in a sample when it is combusted in a sealed, high-pressure oxygen chamber surrounded by water. Heat of combustion is determined by multiplying the temperature rise by the heat capacity determined from the standardization with a benzoic acid tablet**.** Further caloric corrections were then made to account for leftover fuse wire and ash. All values are reported as calories/g dry weight. Not all species were collected during each sampling month, resulting in variable sample size between species across months. Due to low sample weight of bay anchovy and white trout samples, we combined samples of the same species, with similar weight, length, and same collection month one sample for use in the Parr Bomb Calorimeter.

Data Analysis

Variation in the dry energy density (calories/g) of gulf menhaden and Atlantic croaker were modeled using length, month, age, state of collection, and the magnitude of Mississippi river discharge in the preceding month as predictor variables. Age class was assigned to samples using a fork length threshold unique to each species. Gulf menhaden with a fork length longer than 150 mm were categorized as adults, and those shorter than 150mm were categorized as juveniles (Lewis & Roithmayr, 1981). Atlantic croaker with a total length longer than 140mm were categorized as adults, and those shorter than 140mm were categorized as juveniles (White & Chittenden, 1977). We derived monthly values of the mean Mississippi River discharge (m^3/s) for the region from the U.S. Army Corps of Engineers (USACE) monitoring station (www.mvn.usace.army.mil) at Mississippi River Mile 306.3 (31° 00′ 30′′ N, 91° 37′ 25′′W), approximately 121 km north of Baton Rouge. A series of ANOVAs followed by post-hoc Tukey tests were used to assess differences in dry energy density of gulf menhaden and Atlantic croaker based on the age, state of collection, and the month of collection. Linear regression was used to assess if the relationship between fork length and dry energy density of gulf menhaden and Atlantic croaker differed between seasons of collection (spring, summer, fall). The relationship between Mississippi river discharge and dry energy density of gulf menhaden and Atlantic croaker was also tested with linear regression, with gulf menhaden compared between age classes. The above analyses were not possible for bay anchovy and white trout due to limited sample quantity and distribution temporally, but we report descriptive calculations of dry energy density for these fish species.

Results

The calorimetric analysis indicated that the dry energy densities of bay anchovy and white trout ranged from 3925 to 4387 calories/g (4261 calories/g ± 126 SD, n = 74) and 3118 to 4581 calories/g (4120 calories/g ± 358 SD, n = 30) respectively. Bay anchovy and white trout analyzed also varied in fork length ranging from 40 to 77 mm (49 mm ± 9 SD, n = 74) and 48 to 121 mm (78 mm ± 18 SD, n = 30).

The dry energy densities of gulf menhaden ranged from 2578 to 6821 calories/g (5069 calories/g ± 794 SD, n = 193) and the fork length ranged from 82 to 315 mm (158 mm ± 30 SD, n = 193). ANOVA results indicated that month of collection ($F(8, 175) = 2.966$, $p = 0.004$) and age ($F(1, 175) = 66.443$, $p < 0.001$) had significant effects on dry energy density, but did not interact ($F(8, 175) = 0.901$, $p = 0.517$). Adult gulf menhaden (5483 calories/g ± 670 SD, n = 106) have higher dry energy densities than juvenile gulf menhaden (4566 calories/g ± 627 SD, n = 87; Tukey's

HSD Test, $p < 0.001$, Figure 1). Additionally, dry energy densities peaked during the month of September (5610 calories/g ± 615 SD, n = 35) and were at their lowest during the month of May (4546 calories/g ± 495 SD, n = 14; Tukey's HSD Test, $p < 0.001$, Figure 1).

The dry energy densities of Atlantic croaker ranged from 3021 to 6445 calories/g (4524 calories/g ± 646 SD, n = 129) and the total length ranged from 50 to 230 mm (146 mm ± 39 SD, n = 129). ANOVA results indicated that month of collection ($F(10, 92) = 29.159$, $p < 0.001$) had significant effects on dry energy density. Age was not included in the model due to limited sample size. Dry energy densities peaked during the month of July (5416 calories/g ± 453 SD, n = 17) and were at their lowest during the month of November (3841 calories/g ± 360 SD, n = 14; Tukey's HSD Test, $p < 0.001$, Figure 2). Overall, dry energy density was generally highest in adult gulf menhaden compared to juvenile gulf menhaden and adult Atlantic croaker (Figure 3).

Additionally, a simple linear regression was used to test if length significantly predicted the dry energy densities of gulf menhaden and Atlantic croaker during each of the seasons. Fork length significantly predicted dry energy density of gulf menhaden and the relationship did not vary by season ($\beta = 12.8$, $p < 0.001$, Figure 4). Similarly, total length significantly predicted dry energy density of Atlantic croaker and the relationship did not vary by season ($\beta = 15.0$, $p < 0.001$, Figure 5).

Mississippi River flow rates during the month prior to collection ranged from 242161.3 to 1384900 m^3/s. A simple linear regression indicated that flow rate of the previous month did not significantly impact the dry energy density of juvenile gulf menhaden ($\beta < 0.001$, $p = 0.2357$,

Figure 6) or adult gulf menhaden ($\beta < 0.001$, $p = 0.9182$, Figure 6). However, results indicated that flow rate significantly impacted dry energy density of adult Atlantic Croker ($\beta < 0.001$, $p < 0.001$, Figure 6); dry energy densities were higher following months of higher river discharge.

Discussion

In this work, we aimed to provide caloric density data on four forage fish species found in the GOM: gulf menhaden, Atlantic croaker, white trout, and bay anchovy. These species are important prey for commercially important fisheries such as tuna, grouper, snapper, trout, and red drum (Berenshtein, 2021). We were able to quantify the average dry energy densities of these species, which can be used to improve ecosystem models. We found that gulf menhaden and Atlantic croaker exhibit temporal and age class dependent variation in their dry energy densities. Furthermore, a strong positive relationship was found between fish length and the dry energy densities of gulf menhaden and Atlantic croaker, but this relationship did not change by season. Finally, we found that Atlantic croaker had slightly higher dry energy densities following months of higher river discharge.

Existing literature provides single estimates of energy density for each of these four species except white trout. Gulf menhaden have been analyzed using a dry energy density of 5,376 calories/g (Russell, 2004). Our reported gulf menhaden mean dry energy density is comparable to past studies (within 6%). In previous studies, Atlantic croaker have been analyzed using a dry energy density of 4638 calories/g (Russell, 2004). Our reported Atlantic croaker mean dry energy density is highly comparable to this existing value (within 3%). Bay anchovy in the

Chesapeake Bay is reported to have a wet energy density of 1000 calories/g (Luo & Brandt, 1993) and a water content of 81% (Dongbang & Wiwattanasirikul, 2015), resulting in an estimated dry energy density of 5623 calories/g. Additionally, a dry energy density of 5,395 calories/g has been used for bay anchovy found in the Gulf of Mexico (Russell, 2004). Our reported bay anchovy mean dry energy density is much lower than past reported energy densities (20-25% lower). This difference is perhaps a result of sampling technique, location, or sample processing. We were unable to find a reported energy density for white trout; however, our reported white trout mean dry energy density is comparable to that of bay anchovy, gulf menhaden, and Atlantic croaker suggesting that it is a reliable estimate of dry energy density for this species.

We also investigated if the dry energy densities of gulf menhaden and Atlantic croaker are related to total length and age. Previous work has found that juvenile Atlantic croaker have a relationship between lipid content (%) and total length, with longer fish having a higher lipid content (Schloesser & Fabrizio, 2017). Our results found that juvenile Atlantic croaker had lower dry energy densities than adults, and in both juvenile and adult Atlantic croaker longer individuals had a higher dry energy density suggesting that changes in caloric content are at least in part due to the increased lipid content that co-occurs with growth. Similarly, it has previously been documented that juvenile and subadult gulf menhaden have increased lipid content in comparison to larval gulf menhaden (Deegan, 1986). Gulf menhaden and Atlantic croaker are lipid rich, migratory fish species so we expected these species to follow similar trends in lipid storage and energy density. Our results found, that like Atlantic croaker, adult gulf menhaden had higher dry energy densities, and in both juvenile and adult gulf menhaden larger individuals had higher dry energy densities, suggesting that the changes in caloric content are in part due to changes in lipid storage rates that occur during growth and development. The consequence for ecosystem models is that the prey biomass will be of lower nutritional value for predators that feed mainly on juvenile fish and higher for those predators that feed mainly on adult fish.

Additionally, we investigated if dry energy densities of gulf menhaden and Atlantic croaker are related to the month of collection. Previous studies have examined the temporal variation of lipid content of juvenile Atlantic croakers and found that lipid content steadily increases throughout the spring and summer, peaking just before migration in the fall, and decreases rapidly during the migratory season and remains steady until the next spring when the cycle repeats (Schloesser & Fabrizio, 2016). Our results show a similar trend, where dry energy density increases during the winter, spring, and early summer, peaking in July or August, and then decreases during the late summer and fall. The shift in timing of storage and depletion may be due to a difference in location, as our study was conducted in the Gulf of Mexico and the previous study was conducted in the Chesapeake Bay; this also suggests that Atlantic croaker in the Gulf of Mexico and the Chesapeake Bay migrate and spawn at different times of the year. Similarly, gulf menhaden experiences temporal variation in lipid content, with lipid content being higher in the fall pre-migration in comparison to in the spring post-migration (Leaf et al., 2018). Our results show a similar trend where dry energy density increases throughout the spring and summer and decreases throughout the fall; thus, suggesting that changes in caloric density of gulf menhaden is due to storage of lipids in preparation for migration and depletion of lipids during migration. The consequence for ecosystem models is that prey biomass will be of lower nutritional value to predators that feed offshore or in the fall and winter than to predators that feed onshore in the spring and summer.

Finally, we investigated if dry energy densities (calories/g dry weight) of gulf menhaden and Atlantic croaker are related to the magnitude of Mississippi River discharge. Gulf menhaden lipid content was found to be positively correlated to spring river discharge when analyzed at a yearly scale (Leaf, 2017). This was hypothesized to be a result of increased nutrient flow via freshwater inputs that increased fishery production. We expected that this trend would hold true at a narrower monthly scale with dry energy density being higher in months following high discharge for both gulf menhaden and Atlantic croaker. However, our results indicated that Mississippi River discharge had no effect on the dry energy density of gulf menhaden, while Atlantic croaker had slightly higher dry energy density following higher discharge months. One reason for the discrepancy in results is the scale of analysis. The previous study looked at the impact of spring river discharge on the lipid content for the year, whereas our study focused on month-to-month variation. It is possible that a trend was not detected due to the trophic delay in incorporating nutrient inputs into the ecosystem. Additionally, it is also possible that Mississippi river discharge has a greater impact during months of high production like the spring and summer, which means that high discharge during winter months would not result in the same levels of fishery production. Ultimately, ecosystem models should incorporate the relationship between caloric density and annual variation in climate, but monthly variation in weather is much less important in determining the caloric content of forage fish species in the GOM.

While the descriptive caloric information about GOM forage fish is valuable on its own, the caloric data could be incorporated into ecosystem models to increase their accuracy and improve management recommendations. Past studies in other marine ecosystems have incorporated prey quality data into their ecosystem models; for example, an ecosystem model for the Alaskan Gyre incorporate prey caloric data to model the coastal production and growth of Pacific salmon (Aydin et al., 2005). However, the current ecosystem model for the Gulf of Mexico relies on biomass and does not incorporate prey quality data (Geers et al., 2016). Past studies have found that when caloric information is incorporated into prey analysis, high energy density prey items such as fish and shellfish increase in diet importance relative to low energy density prey items (McCawley & Cowan, 2007). Logically, the same pattern would hold true when species specific caloric information is included; high energy density fish species would increase in diet importance in comparison to low energy density fish species. This suggests that the current GOM ecosystem model underestimates the importance of high energy density fish like gulf menhaden and Atlantic croaker in the diets of economically valuable predator species such as, dolphins, seabirds, sharks, tunas, groupers, snappers, trout, and red drum (Berenshtein, 2021). It is our hope that future research will incorporate our caloric data about these common Gulf of Mexico forage fish species into existing the biomass-based model to aid management decisions for economically valuable game fish and conservation of megafauna.

Table 1 Summary of species, locations (state waters), and years of collection used in this study.

Species	Location	Year	n
Atlantic croaker	Mississippi	2018	77
		2019	42
		2022	10
Bay anchovy	Mississippi	2018	55
		2022	19
Gulf menhaden	Alabama	2017	15
	Louisiana	2017	25
		2017	20
		2017	20
		2017	17
	Mississippi	2016	8
		2017	45
		2018	19
	Texas	2017	24
White trout	Mississippi	2017	15
		2018	15

Figure 1. Boxplot of monthly patterns of dry energy density (calories/g) of gulf menhaden. White boxes are juvenile fish (fork length < 150 mm, n = 87) and gray boxes are adult fish (n = 106). Dark lines in each box represent median values, the box is the interquartile range (IQR, 25th to 75th percentile values), and whiskers are range of the data, up to 1.5 X the lower and upper IQR. Those data outside the range of the whiskers are plotted as points.

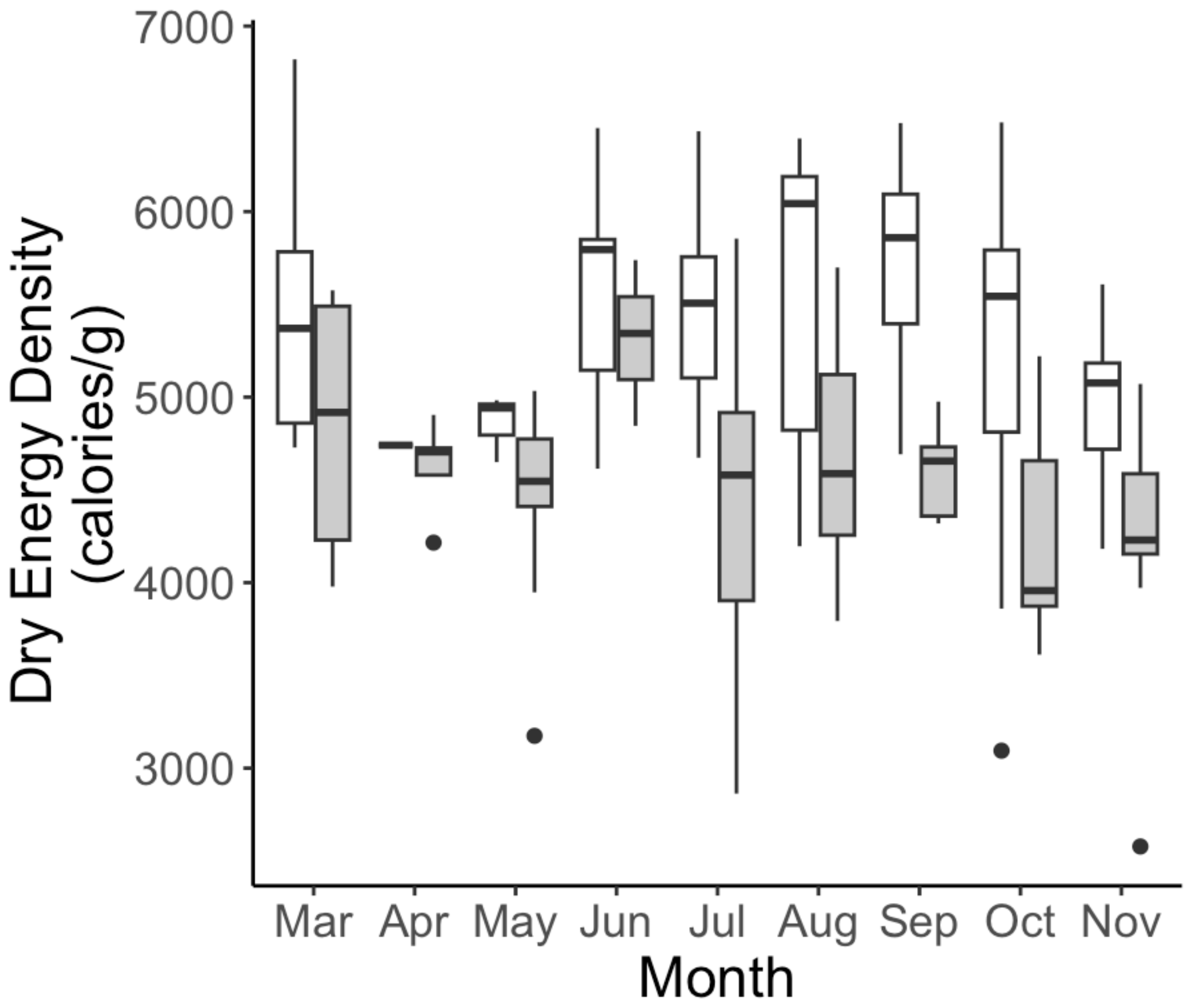


Figure 2. Boxplot of monthly patterns of dry energy density (calories/g) of adult Atlantic croaker (n = 103). Dark lines in each box represent median values, the box is the interquartile range (IQR, 25th to 75th percentile values), and whiskers are range of the data, up to 1.5 X the lower and upper IQR. Those data outside the range of the whiskers are plotted as points.

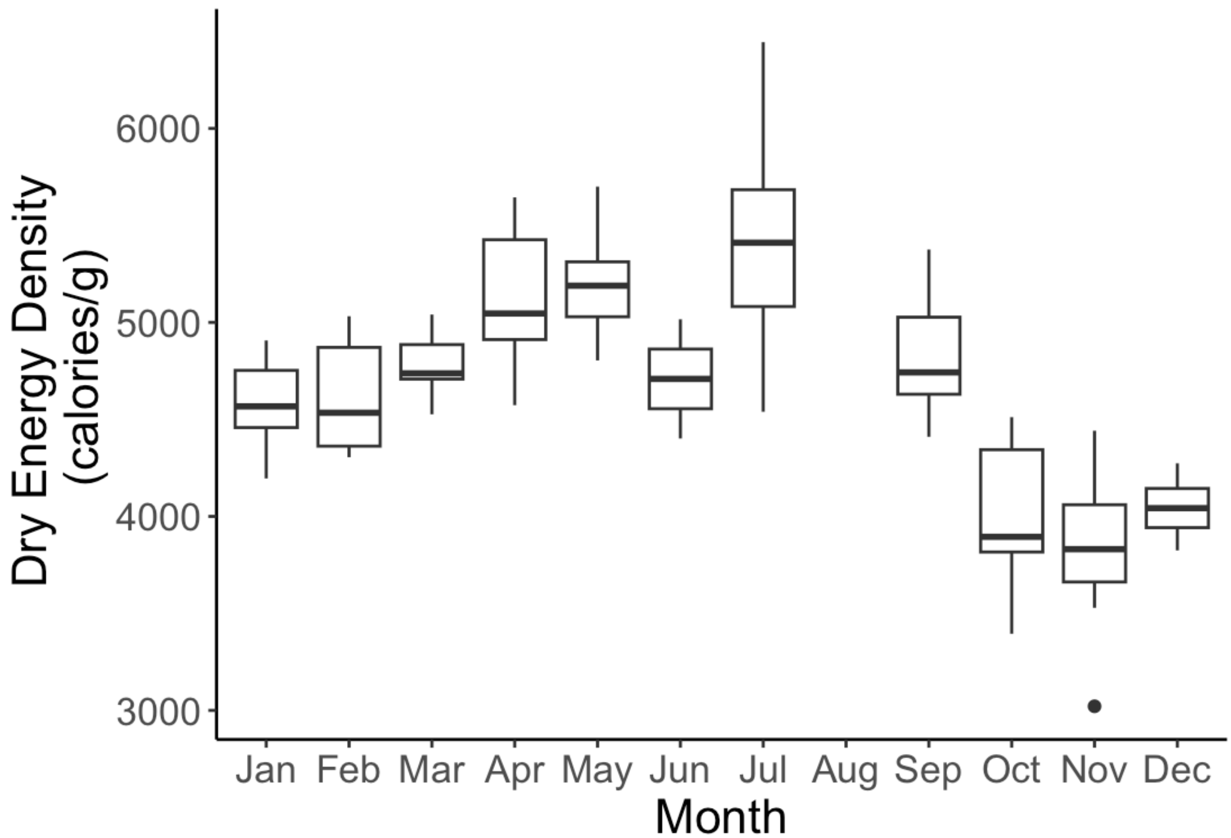


Figure 3. Monthly patterns in dry energy density (calories/g) of adult Atlantic croaker (open circles, dashed line), adult gulf menhaden (black circles, black line), and juvenile gulf menhaden (grey circles, grey line).

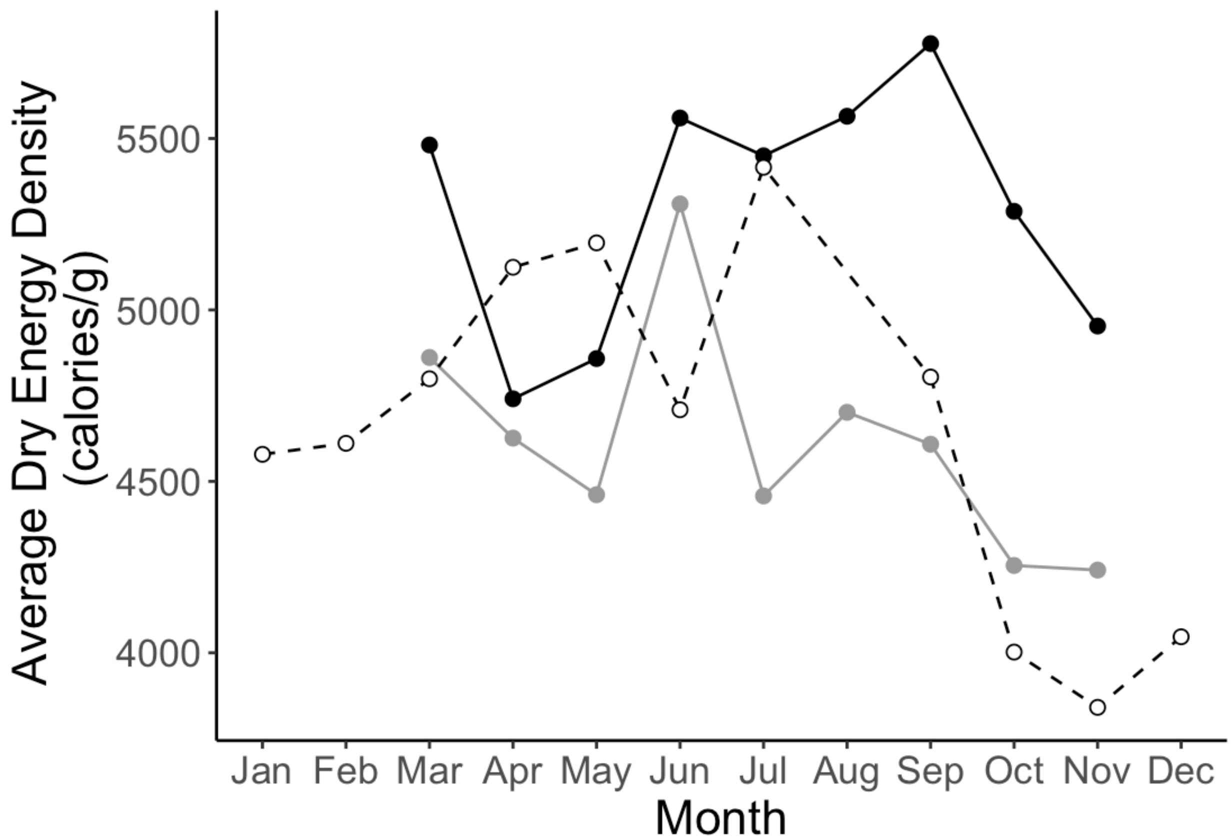


Figure 4. Scatterplot and linear relationship of dry energy density (DED) (calories/g) and fork length (FL) (mm) in gulf menhaden by season. Fall (open points), Spring (grey points), Summer (black points). The solid line is the linear model for all seasons combined.

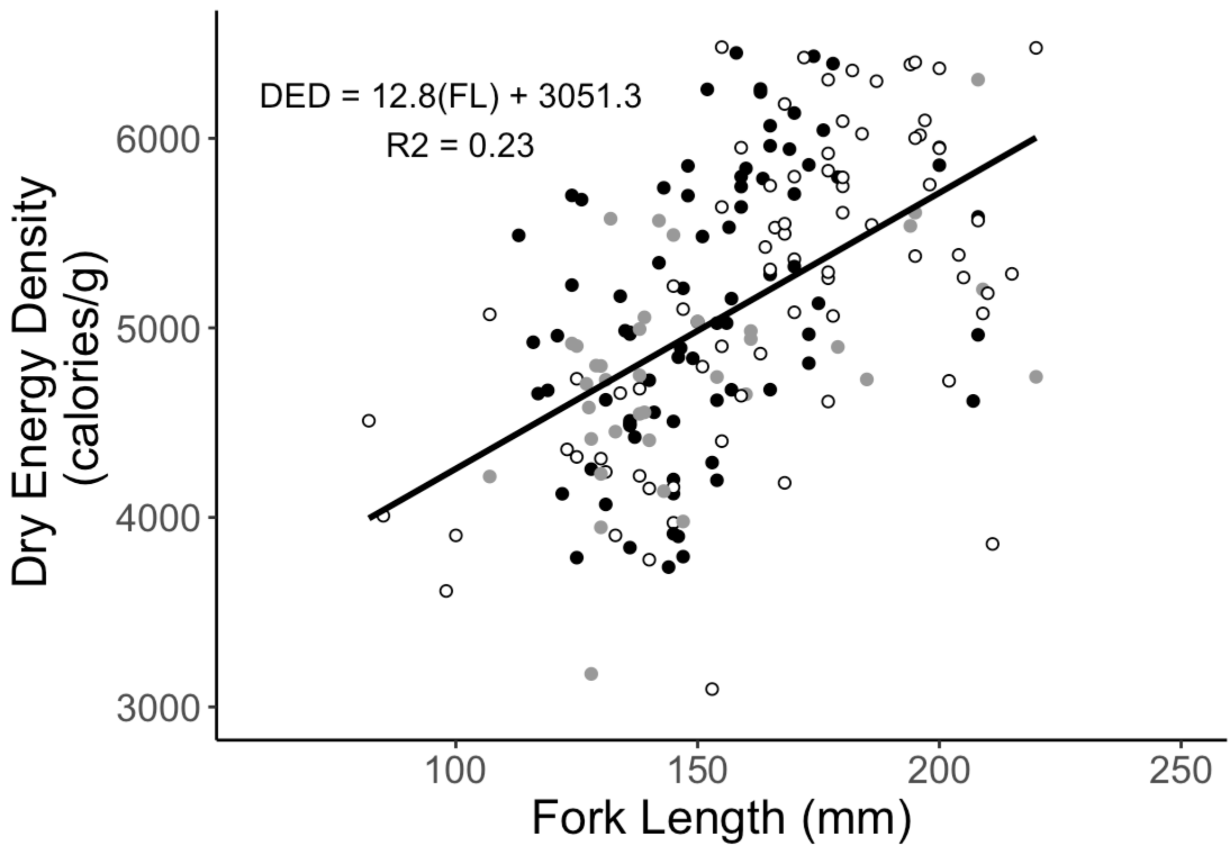


Figure 5. Scatterplot and linear relationship of dry energy density (DED) (calories/g) and total length (TL) (mm) in Atlantic croaker by season. Fall (open points), Spring (dark grey points), Summer (black points), Winter (light grey points). The solid line is the linear model for all seasons combined.

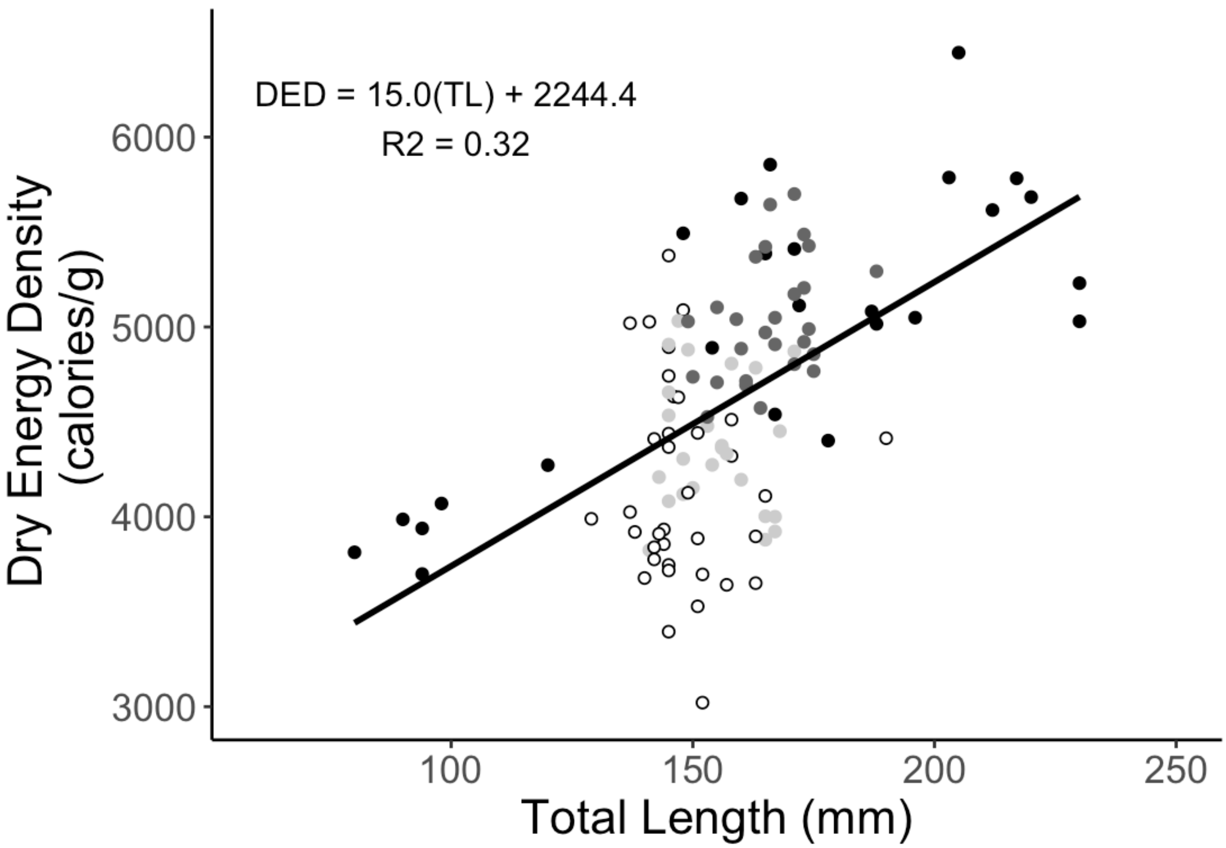
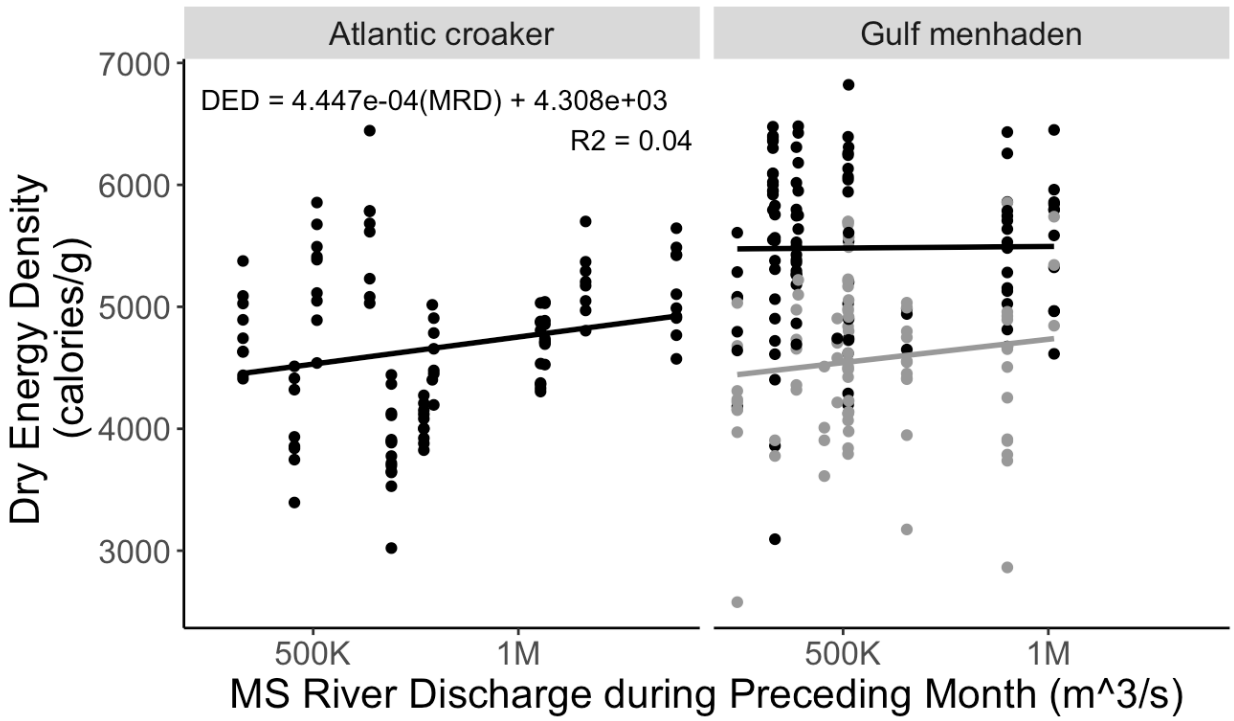


Figure 6. Scatterplot and linear relationship of dry energy density (DED) (calories/g) of gulf menhaden and Atlantic croaker in relation to the Mississippi River discharge (MRD) of the preceding month (m^3/s). Adults are shown in black, and juveniles are shown in grey for gulf menhaden.



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